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Differential organization of taxonomic and functional diversity in an urban woody plant metacommunity

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Abstract

Questions: Urban ecosystems present an opportunity to study ecological communities in the context of unprecedented environmental change. In the face of urban land conversion, ecologists observe new patterns of species composition, dominance, behaviour and dispersal. We propose a hypothetical socioeconomic template that describes a gradient in human investment in community composition to aid in organizing the human role in shaping urban biodiversity. We asked: (1) what is the relative magnitude of taxonomic and functional turnover of urban woody plant communities across different land-use types; and (2) do land uses exhibiting higher intensity of human management of biodiversity support higher turnover over those with less human influence?

Location: Baltimore, MD, USA (39°17′ N, 76°38′ W).

Methods: We examined patterns in woody plant biodiversity across 209 plots of different urban land uses. Six land-use types were arranged along a gradient in the intensity through which humans are hypothesized to manage species composition at the plot scale. We calculated local, or α-diversity, and compositional turnover, or β-diversity, of taxonomic and functional diversity across plots within each land-use type. We compared the magnitude of these biodiversity measures between land uses to test our conceptual template for how the intensity of human management can predict urban woody plant biodiversity.

Results: We observed high taxonomic turnover in residential and commercial plots compared with vacant or open space land-use areas. This was associated with a weaker, but similar, pattern in functional diversity. This was associated with low total abundance in residential and commercial plots. Furthermore, the number of unique species was extremely high in the same land-use types.

Conclusions: Our observations help explain why turnover can be high in heavily managed plots relative to vacant land. In patches without heavy human management, we found low levels of turnover. This highlights the importance of assessing diversity both locally and at the level of turnover between patches. Management and policy can benefit from the perspective embodied in the conceptual approach tested here.

Introduction

A fundamental goal of community ecology is to understand the mechanisms that maintain species co-existence at multiple spatial scales. In the rapidly urbanizing landscape, the processes that maintain local and regional species diversity, as well as turnover in composition, involve not only general ecological mechanisms (e.g. the productivity hypothesis (Gaston 2005), the ecosystem-stress hypothesis (Menge & Sutherland 1987) and the intermediate disturbance hypothesis (Connell 1978)), but also newly considered drivers of diversity and composition best explained by human behaviour and decision-making (Williams et al. 2009; Aronson et al. 2014). Urban places exhibit a juxtaposition of patch types that support a wide variety of ecological communities, governed by a range of socioecological processes (Cadenasso et al. 2007; Lososová et al. 2011). Such patches can include remnant habitats, such as wooded riparian or park areas and other unmanaged areas such as roadside plant communities, which are

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often, but not necessarily, interpreted as 'disturbed' environments. Urban habitat patches also include designed landscapes, such as lawns and managed parks and gardens. Including these managed and designed green spaces in calculations of biodiversity is important, as privately owned and maintained gardens and yards can constitute the majority of available urban green space (Goddard et al. 2010). The biodiversity in each location is assembled as a result of both indirect and direct effects of human activity on the landscape (Bonthoux et al. 2014).

In general, urban biodiversity is described at either local or regional scales, with relatively less focus on variation in diversity *within* cities, between habitat patches arranged along urban environmental, management and spatial gradients (Knapp et al. 2010; Ferenc et al. 2013; McDonnell & Hahs 2013; but see Godefroid 2001; Thompson et al. 2003; Celesti-Grapow et al. 2006; Ricotta et al. 2012; Gutiérrez-Cánovas et al. 2013; Ramalho et al. 2014; Beninde et al. 2015). Local species diversity, or α-diversity, represents a subset of the regional species pool (γ-diversity). Shifts in species composition from one local assemblage to another represent species turnover, or β-diversity. Regional species diversity is therefore comprised of not just local diversity, but also of compositional turnover. This classic concept is powerful to embrace in the context of urban ecosystems for a number of reasons. First, it highlights that local communities are not isolated on the landscape, but connected to a common regional species pool, i.e. they are members of a metacommunity (Leibold et al. 2004). Furthermore, this common regional species pool is not limited to just native species, but also non-native, potentially invasive taxa as well. Second, it emphasizes composition as an important regulator of how biodiversity emerges at larger scales. Compositional change from one location to the next can result from many classically invoked biotic and abiotic factors, such as competition and environmental constraints (Leibold et al. 2004). However, shifts in both diversity and composition in cities can also be linked to a variety of socioeconomic factors, such as human-mediated dispersal (Hope et al. 2003; Kinzig et al. 2005; Bigirimana et al. 2012; van Heezik et al. 2013; Belaire et al. 2014; Clarke & Jenerette 2015). Despite recognition of this, integration of these observations into a testable, multi-scale conceptual model of biodiversity for urban ecosystems is still lacking.

Species vary in their dispersal ability. In urban ecosystems, people not only actively move species around, regardless of their innate dispersal abilities, but also facilitate the establishment of very vagile species (Albrecht et al. 2011; McConkey et al. 2012; von der Lippe & Kowarik 2012). Dispersal rates between patches in the urban landscape alter the relative contribution of local diversity and compositional turnover to overall regional diversity patterns (Mouquet & Loreau 2003; Aicher et al. 2011; Schleicher et al. 2011). In general, as dispersal increases, local assemblages become saturated with species from one common regional species pool, decreasing turnover but increasing local diversity (Mouquet & Loreau 2003). Eventually, without localized disturbances or high levels of local environmental heterogeneity, more competitive species become dominant in patches, resulting in a decline in regional diversity. In urban ecosystems, high levels of dispersal by the total pool of species favoured by urbanization and destruction or alteration of native habitats generally has led to a shift towards species pools dominated by stress-tolerant and broader dispersing species (Williams et al. 2009). Taken together, these shifts contribute to widely documented patterns of biotic homogenization and the hypothesized decline in urban regional diversity (Lososová et al. 2012; Ricotta et al. 2012; Aronson et al. 2014). However, we know diversity does not always decline in urban environments (Kowarik 2011; Aronson et al. 2015). Compositional turnover, or β-diversity, and interspecific variation in dispersal abilities may help us understand why this occurs.

Community assembly is generally conceived as the processes by which species co-occur locally as a subset of the regional species pool (Leibold et al. 2004). In urban environments, abandoned or remnant habitats can be conceived of as being 'self-assembled', in that the community assembly process is similar to non-urban ecosystems, primarily as a result of interactions between the existing community and environmental characteristics (Fig. 1). But many assemblages occur in the urban landscape primarily as a function of a multitude of socioeconomic processes, such as gardens, yards or managed parks. Therefore, we propose a hypothetical socioeconomic template that describes a gradient in human investment in community composition to aid in organizing the human role in the community assembly process (Fig. 1).

Where social investment is low, composition and/or diversity is not a priority or is ignored and the harsh urban geophysical template imposes strong environmental filtering (Calfapietra et al. 2015), therefore leading to low compositional turnover (e.g. Chase 2007). However, as socioeconomic investment in practice increases, focus may turn to conservation of existing communities or habitats, restoration activity and the design of novel ecological communities. In this case, humans impose substantial constraints on the assembly process, either by altering habitat to promote the desired species composition, or by directly assembling, eliminating and/or maintaining certain species combinations. We term these communities as undergoing 'facilitated assembly' (Fig. 1; Swan et al. 2011). One prediction is that, among such habitats, turnover is predicted to be quite high because of differential human

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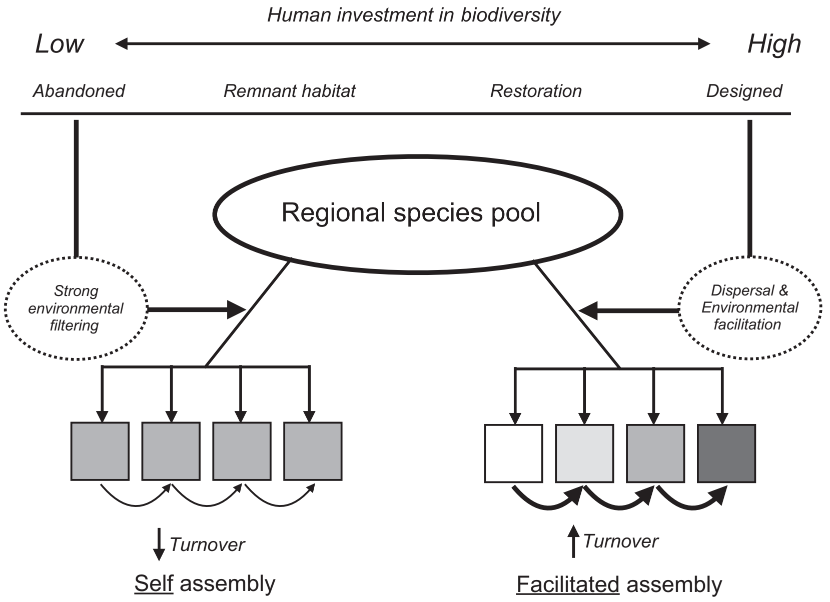

Fig. 1. A conceptual model of the influence of human investment on the development turnover, or β-diversity, in urban ecosystems. Self- and facilitated assembly describe processes selecting subsets of species combinations from the regional species pool. Here, control on assembly is hypothesized to be governed by biological interactions mediated by the geophysical template or local human perception and behavior. Strong environmental filtering should constrain species composition regardless of level of human input, given consistently harsh environmental conditions (left). This should reduce species turnover, as indicated by the smaller arrows. Heterogeneity in habitat conditions among parcels and/or the facilitation of species coexistence directly via aided dispersal (e.g., planting, attraction/elimination of undesirable taxa) or indirectly via habitat alteration, should lead to the development of β-diversity (larger arrows). Modified from Swan et al. (2011).

decision-making and preferences (Kendal et al. 2012; Avolio et al. 2015; Johnson et al. 2015). High rates of turnover, particularly between communities with high levels of socioeconomic input, may lead to higher than expected regional diversity when taking such designed communities into account.

To test this concept, we examined patterns in woody plant biodiversity across a variety of urban human land uses, where land use was arranged along a gradient in the intensity through which humans are hypothesized to manage species composition at the parcel scale. We focused primarily on β-diversity, at taxonomic and functional levels. We predicted that taxonomic turnover should be highest in areas where humans have very large control over composition. We expected functional turnover differences to be weak, given regional-scale constraints on traits compatible with the urban environment (Reichard & White 2001; Pataki et al. 2013; Calfapietra et al. 2015).

Methods

Study sites and tree communities

We made use of a large data set created as a part of a tree inventory effort in the Baltimore Metropolitan Region, USA. Forest composition of planted and naturally recruited individuals were identified to species using plot-based random sampling (Nowak et al. 2008, http://nrs.fs.fed.us/-data/urban/; $N = 209$). Dates of inventories ranged from 1999 to 2009. The number of inventory plots varied by land-use (Table 1), and land-use was noted during sampling, with designations following the USDA Forest Service's I-Tree Eco User's Manual (v 5.0, www.itreetools.org). Plot size was 0.04 ha, and all individuals 2.54 cm DBH or more were counted and identified.

Our hypotheses rely on a gradient of increasingly active management of species composition (Fig. 1). As such, we interpret the land-use descriptions in light of this (Table 1), and present them in order of predicted low to high human investment in and management of local species composition and diversity: Vacant Lots, Open Space, Parks, Institutional, Commercial, Residential. While certainly Vacant Lots reflect no current active management of local species composition, parcels categorized as Institutional, Commercial and Residential do. Open Space and Parks, however, likely represent a mix. We place these two in between the identified end members, and interpret the results in light of some ambiguity in the order of these categories. We maintain, however, that given the information associated with the data set and the large number of replicates within each land-use type (Table 1), including these land-use types was more valuable than excluding them.

Table 1. Land-use classes as defined by Cadastral Geodatabase LANDUSE.TaxParcel Data Dictionary. The number of plots in each land-use class included in the study are also given (*n*).

Land Use	*n*	Description
Vacant Lots	16	Parcel that does not have a principal building, at least 10 yr since created through the subdivision process, and is not predominantly covered with accessory uses such as garages and swimming pools. Also includes unbuildable land
Open Space	55	Unimproved space transferred to the local government through the development process or acquired by other means; space that contains surface or underground water storage and also provides open space/recreational amenity
Parks	16	Maintained space containing a permanent recreational improvement
Institutional	20	Places of worship, colleges/schools, medical facilities, police/fire, cemeteries, libraries, other government facilities
Commercial	14	Structure containing retail/service or office uses. Includes parking lots
Residential	88	Single-family detached, attached or multi-family (3+) homes

Functional data

Functional trait data were collected that describe how plant species cope with general ecological challenges in dispersal, establishment and persistence (Weiher et al. 1999). Traits for all species were assembled from online databases (Zanne et al. 2009 http://hdl.handle.net/10255/dryad.235; USDA PLANTS Database, USDA, NRCS 2013 http://plants.usda.gov). They included leaf retention, relative growth rate, re-sprouting ability, rate of vegetative spread, height at maturity, seed mass and wood density (Table 2). These traits were chosen due to their availability for the species under study, and how well they reflect strategies in dispersal, seedling growth, seed production, competitive ability, acquiring and holding space, and response to disturbance (Table 2; Weiher et al. 1999; Diaz et al. 2004).

Local diversity

Local (α) taxonomic diversity was calculated as Shannon diversity (H′) for each plot. Local functional diversity required dealing with both categorical and continuous traits (Table 2). Continuous traits were range-standardized, and wood density was $\log_{10}$ transformed to ensure a normal distribution of values. We used the index of functional dispersion (Rao's Q) on a Bray-Curtis dissimilarity matrix, which weights the distances by species abundances, to describe the local diversity of functional traits (Laliberté & Legendre 2010).

Compositional turnover

We analysed turnover, or variation in community composition among plots within land-use types, using the betadisper function in R (R Foundation for Statistical Computing, Vienna, AT). This is an analysis of multivariate homogeneity of group dispersions, and an analogue of the univariate Levene's test for homogeneity of variance (Anderson et al. 2006). This procedure employs a permutation test based on 999 randomizations, resulting in a P-value associated with an F-test comparing the degree of dispersion among principal coordinates to group-level medians. The value of this approach is that it accepts any distance matrix. Compositional turnover in taxonomic diversity was estimated on a Bray-Curtis dissimilarity matrix. Functional turnover was based on Gower's distance as it accepts both categorical and continuous variables (Table 2; de Bello et al. 2013).

Data analysis

Local diversity (Shannon H′, Rao's Q), turnover for both diversity levels, and total abundance per plot were analysed with a one-way ANOVA with land use as the source of variation. We further compared the community-weighted means (CWM) of individual functional traits between land-use types using a one-way ANOVA. *Post-hoc* comparisons between the six land-use classes were estimated, with significance evaluated after adjusting the Type I error rate using Tukey's HSD. All analyses were carried out in the R statistical computing environment.

Results

Abundance and local diversity

Total abundance varied significantly with land use ($F_{5,203}$, $P < 0.001$), with Vacant Lots harbouring significantly more individuals than Residential plots (Fig. 2). Institutional, Commercial and Residential plots, land-use types with clear indications of human management, supported four to eight individuals per plot, while Vacant Lots, Open Space and Parks harbored 17–21 individuals (Fig. 2). Vacant Lots, Open Space and Parks appeared, however, to offer minimal to no human influence on species composition (Table 1).

Patterns in α-diversity largely mirrored those of abundance (Fig. 3, left). Local taxonomic and functional diversity declined with the level of active human management (Fig. 3, left). This was pronounced between Vacant Lots

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Table 2. Traits and references. After Weiher et al. (1999).

Trait	Ecological Challenge								Units	Reference
	Dispersal in Space	Dispersal in Time	Seedling Growth	Seed Production	Competitive Ability	Acquiring Space	Holding Space/ Longevity	Response to Disturbance		
Leaf Retention								X	Binary	USDA PLANTS
Relative Growth Rate			X						Slow Moderate Rapid	USDA PLANTS
Re-sprouting Ability								X	Binary	USDA PLANTS
Vegetative Spread						X			None Slow Moderate Rapid	USDA PLANTS
Height at Maturity					X				m	USDA PLANTS
Seed Mass	X	X	X	X					log(g)	USDA PLANTS
Wood Density					X		X		$kg{\cdot}m^{-3}$	Zanne et al. (2009)

and Residential plots. Shannon diversity was more than twice as high in Vacant Lots, Open Space and Parks compared to the remaining, more actively managed plots. While there was a significant effect of land-use on taxonomic diversity (Table 3), the effect was only weakly significant ($P < 0.1$) for functional diversity. The observed trend, however, was similar, with the lower observed functional diversity levels in Institutional, Commercial and Residential plots. The relatively weaker inter-group functional differences caution any strong interpretation of the broader distinctions drawn for abundance and taxonomic diversity.

Compositional turnover

We observed a consistent pattern of increasing turnover along the hypothesized land-use gradient for both taxonomic and functional β-diversity, with the pronounced differences observed between Vacant Lots and Residential parcels (Fig. 3, right). However, the magnitude of the effect of land-use varied among the diversity dimensions, with taxonomic turnover significant ($P < 0.05$), and functional turnover marginally so at $P < 0.1$ (Table 4). Taxonomic turnover, while generally higher in Institutional, Commercial and Residential plots, was lowest in Parks. Residential plots were the only land-use category with the predicted effect of design elements (Table 1) having statistically higher turnover compared to those categories lacking this feature (Vacant Lots, Open Space, Parks; Fig. 3). Functional turnover showed the weakest patterns among land-use categories, with the largest difference, again, between Residential plots and Vacant Lots and Open Space. Residential Lots exhibited the highest turnover in trait composition. An analysis of the CWMs of individual traits revealed significant differences among certain land-use types. Of the 12 traits/trait states examined, we observed significant variation in four (Table 5). We observed significant variation explained for height at maturity (highest in Parks), seed mass (also highest in Parks), proportion of the community exhibiting rapid vegetation spread (highest in Commercial) and proportion of the community exhibiting leaf retention; there were no evergreen taxa in Vacant Lots compared to the highest number observed in Residential plots (Table 5).

Compositional turnover was examined further by enumerating the number of unique taxa occurring in each land-use category across all plots (Fig. 2, bottom). Residential plots harboured by far the most unique taxa, followed by Open Space, with >16 each. Among the other categories, less than five unique taxa were supported in each (Fig. 2, bottom).

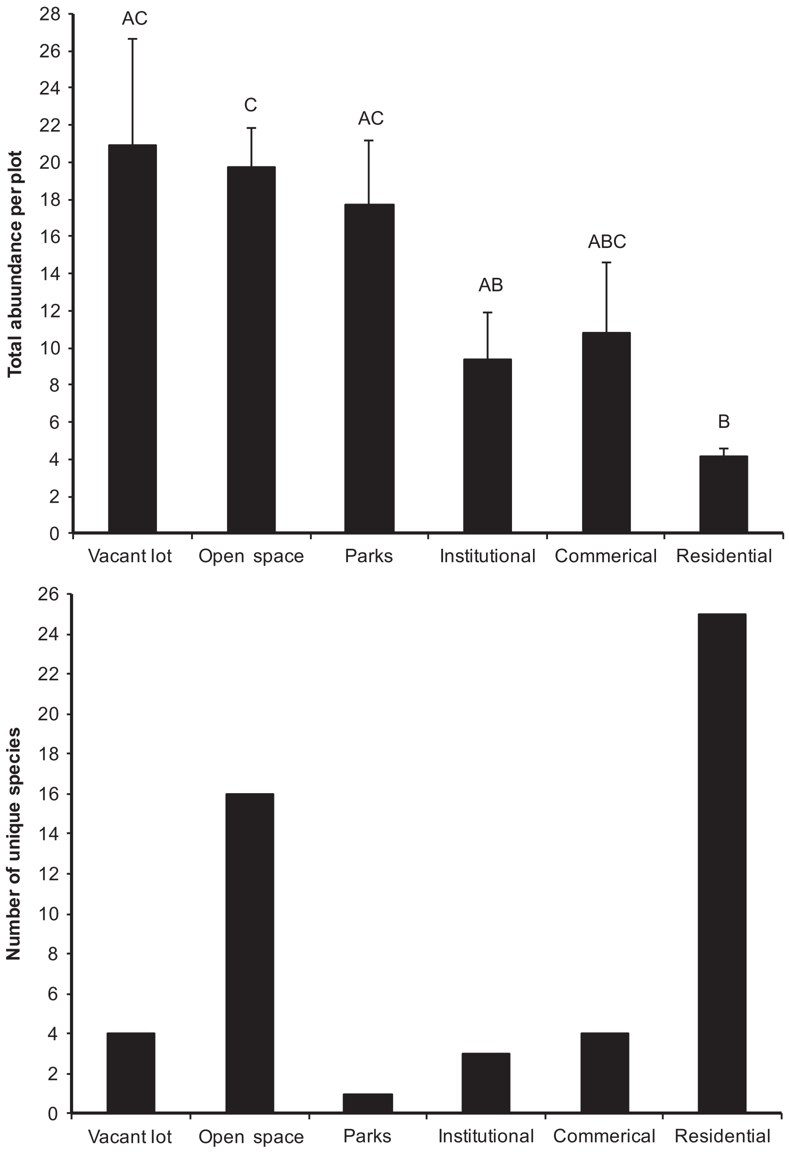

Fig. 2. Mean total abundance per plot, + 1 SE (top). Bars with the same letter are not statistically different following Tukey's HSD ($P > 0.05$). Number of unique species identified in each land use (bottom).

Discussion

In general, the pattern of compositional turnover was consistent with our predictions. We observed high turnover in Residential and Commercial parcels compared with Vacant or Open Space land-use areas. These results can be interpreted in light of two observations. The first is that abundance was very low in Residential and Commercial plots, therefore keeping local diversity low. The second was that the number of unique species was extremely high in the same land-use types. Taken together, these observations can help explain why turnover can be very high in these land-use types relative to Vacant and abandoned land, even though local biodiversity is low.

One interesting pattern we observed is that where the geophysical template was hypothesized to be most harsh (e.g., Vacant Lots, Open Space), higher taxonomic and functional α-diversity was observed, but lower α-diversity was observed in more designed plots. We interpret this in light of total abundance. Simply, humans appear, in this region at least, to prefer few individual woody plants, which consequentially leads to lower diversity. Unlike largely self-assembled habitats, facilitated-assembly plots are more likely to contain single individuals of a species, as

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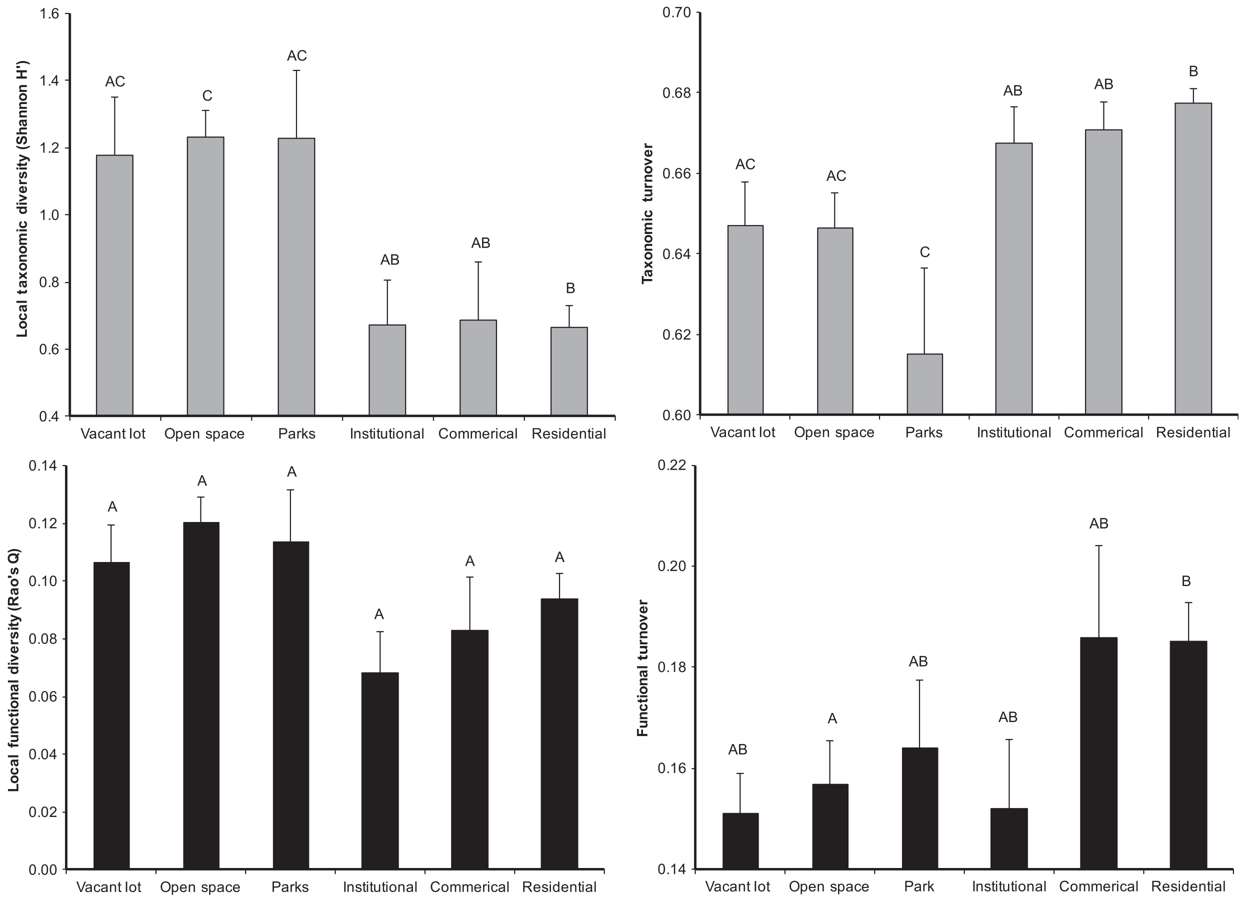

Fig. 3. α (left) and β (right) taxonomic (top) and functional diversity (bottom) for each land use. Units of the *y*-axis for functional turnover are the distance to the centroid in multivariate space. Bars are the mean + 1 SE. Bars with the same letter are not statistically different following Tukey's HSD ($P > 0.05$).

Table 3. Local diversity ANOVA results. *df* = degrees of freedom, SS = sum of squares, MS = mean square, *F* and *P* = *F*-statistic and associated *P*-value for the one-way ANOVA, respectively. Bold values indicate statistical significance at α = 0.05.

Diversity	Metric	Source	*df*	SS	MS	*F*	*P*
Taxonomic	Shannon H'	Land use	5	15.5	3.10	8.86	**<0.001**
		Residuals	203	80.1	0.39		
Functional	Rao's Q	Land use	5	0.042	0.008	1.83	0.109
		Residuals	203	0.935	0.005		

human dispersal allows species to persist in a location at very low population sizes. The variation in the planting or maintenance choices people make from one patch to the next leads to the development of β-diversity. This is in contrast to what may be a more consistent environment in Vacant lots and Open Space, which appeared to support similar local assemblages. Therefore, we suggest abundance and patch-level variation in management choices (or lack thereof) interact to generate divergent patterns in α- and β-diversity in this urban ecosystem. Similarly, high levels of variation in gardens as a result of variation in human planting choices, rather than broader-scale descriptors of landscape context and the environment, have also been found in other cities (Thompson et al. 2003; Jaganmohan et al. 2012; Kendal et al. 2012; Clarke et al. 2014).

We offer two explanations for the weaker response of functional diversity to land use. The first is that, at the regional scale, the urban environment might be selecting for a narrow range of traits regardless of the identity of species that are available for local colonization (McKinney 2006; Vallet et al. 2010). Our analysis of CWMs supports this; even when significant differences were observed, these were between only two land-use classes (Table 5). Even species that are planted and maintained in urban areas remain restricted to some degree by broader climatic and environmental drivers (Ramage et al. 2013). An alternate explanation is that the traits chosen in this analysis are not entirely relevant in the urban environment. For example, there may be other traits that are more important to survival and reproduction in an urban environment than were included here. Traits associated with tolerance to pollution, extremes in temperature or water availability were not included in the analysis, yet may be more important in the urban environment than many of the more commonly reported traits in the general ecological literature (Weiher et al. 1999). Many species that occur in residential, institutional and commercial parcels were likely established on-site as adults, so therefore traits associated with dispersal and, perhaps, establishment, are not necessarily relevant. However, those traits associated with maintaining patterns of growth and fitness in the face of a changing urban environment may be more important to consider, or traits related to human selection of species. For example, Pataki et al. (2013) identified biogeographic origins and leaf phenology traits including leaf N content and specific leaf area, which were predictive of urban ecosystem service traits of interest to city residents, including presence of showy flowers, size at maturity and water requirements. Continuing to establish quantifiable functional predictors of traits that drive human planting preferences will likely increase our theoretical understanding of how urban plant communities are structured.

Other studies that have looked at turnover in taxonomic or functional traits of urban tree communities have also found that changing land use within cities drives a substantial amount of urban forest compositional variation. For example, Bourne & Conway's (2014) study of the Toronto, Canada, urban forest found larger compositional differences between land-use types within municipalities than between municipalities. A study of urban tree diversity in Christchurch, New Zealand (Stewart et al. 2009), in managed and unmanaged parkland and residential properties observed increasing proportions of exotic trees in more managed habitat patches, but also found spatial variation in composition related to sampling proximity to larger remnant woodland patches. Residential land-use patches had higher tree species richness than remnant forest patches in a study of Chongming Island, China, as well as contrasting size structure compared to other land uses (Zhao et al. 2013). To best describe patterns of urban forest diversity, future studies should continue to stratify sampling efforts across land uses within cities, and also further consider how land use interacts with spatial variation in environmental gradients and socioeconomic patterns.

Table 4. β-diversity ANOVA results. Distance to group centroids. *df* = degrees of freedom, SS = sum of squares, MS = mean square, *F* and *P* = *F*-statistic and associated *P*-value for the one-way ANOVA, respectively.

Diversity	Source	*df*	SS	MS	*F*	*P*
Taxonomic	Land use	5	0.073	0.0147	5.90	**0.002**
	Residuals	203	0.508	0.0025		
Functional	Land use	5	0.046	0.0092	2.21	0.055
	Residuals	203	0.850	0.0042		

Table 5. CWMs for each trait studied across land uses. Height, Seed Mass and Wood Density are continuous, with the remaining traits reported as proportion of the total community (see Table 2). Bolded traits are significant at $\alpha = 0.10$, as indicated by a significant one-way ANOVA *F*-test. *F*-statistics are given. To aid interpretation, the minimum and maximum values are bolded. For $P < 0.05$, statistically similar values are indicated with the same letter superscript.

	Vacant Lot	Open Space	Parks	Institutional	Commercial	Residential	$F_{5,205}$
Height	23.5	24.2	**25.8**	**20.6**	22.3	21.5	**2.14***
Seed Mass	1.77^{AB}	1.55^{AB}	**1.87**^{A}	1.79^{AB}	1.49^{AB}	**1.34**^{B}	**2.89****
Wood Density	571.8	552.0	**582.5**	571.6	**533.7**	549.7	0.86
Relative Growth Rate							
Slow	**0.14**	0.17	0.20	**0.24**	0.17	0.20	0.26
Moderate	0.25	0.18	**0.35**	0.22	**0.11**	0.27	1.64
Rapid	0.61	0.64	**0.45**	0.50	**0.71**	0.52	1.78
Vegetative Spread							
None	0.69	0.74	0.77	**0.85**	**0.64**	0.78	1.08
Slow	**0.19**	0.12	0.09	**0.03**	0.15	0.10	1.10
Moderate	**0.04**	**0.14**	0.13	0.11	0.06	0.07	1.04
Rapid	0.09^{AB}	**0.00**^{A}	0.01^{AB}	0.01^{AB}	**0.14**^{B}	0.04^{AB}	**2.65****
Leaf Retention	**0.00**^{A}	0.09^{A}	0.06^{AB}	0.10^{AB}	0.17^{AB}	**0.24**^{B}	**3.00****
Re-sprouting Ability	**1.00**	0.94	0.94	0.93	**0.83**	0.85	1.55

$*P < 0.1$, $**P < 0.05$.

Conclusions

Our results demonstrated that abundance of individuals was higher in patches of low socioeconomic investment, and this was associated with higher local diversity. In areas without human intervention, we found low levels of turnover, suggesting a more homogenized pool of species or saturation from the regional species pool compared to more actively managed patches. This highlights the importance of assessing diversity both locally and at the level of turnover between patches. Management and policy can benefit from the perspective embodied by the conceptual approach offered here. Management decisions might be better informed from observing biotic diversity patterns in habitats ranging from large remnant patches of essentially native vegetation, through managed parcels, to small interstitial habitats wedged between buildings, along transportation corridors or in neglected sites (Pickett 2010). Because there is the potential for connectivity among this wide range of patches, the test of our conceptual approach prompts examining sites that may not usually be considered to provide urban ecosystem services. This highlights the need to determine how self-assembly and facilitated assembly are distributed across urban patch mosaics as key information for management. The effect of altered composition as a result of human restoration or design can be quantified by comparing ecosystem services along gradients of low to high investment. Management can also be prioritized based on knowledge of what patches are able to support self-assembled communities that fulfill needed ecosystem functions, compared to those patches where different kinds of facilitated assembly may be required to meet sustainability goals.

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Conflict of interest

The authors declare no conflict of interest.

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